

## Natural regeneration in tropical forests along a disturbance gradient in South-East Cameroon

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### ABSTRACT

The dynamics of tropical forests are highly dependent on the forest understorey. Understanding its diversity and composition is essential to ensure sustainable management of forest ecosystems. In this study, following a gradient of human disturbance, we analysed the density, diversity and floristic composition of the forest understorey in three land use types of south-eastern Cameroon: a protected area, a selective logging concession and community forests. Vegetation was inventoried in thirty-three permanent one-hectare plots. Woody individuals (tree, shrub, liana) were classified in four strata depending on their diameter: seedling (dbh < 1 cm), sapling (1–9.9 cm), small trees (10–29.9 cm), large tree (≥30 cm). A total of 4,159 individuals (dbh < 10 cm) belonging to 418 species and 232 genera were recorded. They mainly represent tree species (65%) and shade tolerant plants (77%), with diaspores disseminated by animals (74%). Life forms and modes of dissemination were significantly different between land use types. Abundance, species richness and diversity of juveniles varied significantly between strata and land use types: they were globally the highest in plots that have been logged less than five years before inventory. In terms of species composition, the different land use types were not clearly separated, indicating some resilience to disturbance. A low similarity between strata was observed. In all types, most canopy species are light demanding and cannot regenerate in the understorey. This indicates a natural evolution of the forest stands in the absence of silviculture. The presence of species that currently dominate the canopy of these forests will be gradually reduced without human intervention.

### 1. Introduction

Understorey vegetation plays a crucial role in the dynamics of tropical rainforests. Understanding its diversity and composition is essential to ensure sustainable management of forest ecosystems (Carson & Schnitzer, 2008; Kitajima & Fenner, 2000). For example, the absence or low density of juveniles in the forest understorey indicates a poor regeneration (e.g., Steven, 1994, in Panama; Devi Khumbongmayum et al., 2006, in India).

Understorey vegetation represents more than 60% of plant diversity and is a good indicator of forest structure since its composition is directly influenced by the amount of light and precipitation penetrating the canopy and reaching the forest floor (Costa & Magnusson, 2003; Yongo, 2003; Tchouto et al., 2006; Nogueuim et al., 2010; Beina, 2011). Plants

living in the undergrowth can have different strategies in terms of: (i) life forms, determining the structure and architecture of individuals and their position in the environment, (ii) dispersal modes, promoting or limiting the spatial distribution of species (Garwood, 1989; Hopfensperger, 2007), and (iii) light requirements, determining their successional order (Leck, 2003; Leck & Leck, 1998; Leck & Simpson, 2011). At the landscape level, the coexistence of different strategies reflects the resilient nature of the vegetation, and its ability to maintain ecological diversity and sustainability.

Composition and diversity of the understorey vegetation depends on three sources: the seed rain (Alexandre, 1989), the seed bank (Zebaze et al., 2021), and the vegetative potential of the environment (Bose et al., 2016; Schwartz et al., 2017; Downey et al., 2018). The latter, also known as the juvenile bank, can be divided into two strata: the seedling

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stratum and the sapling stratum. The seedling stratum comprises individuals in the first stage of development after seed germination. Conventionally, the seedling stratum is made up of woody individuals less than one metre high (Kupers et al., 2019; Inman-narahari et al., 2016; Denslow and Guzman, 2000) or with a Diameter at Breast Height (dbh) <1 cm (Lipoma et al., 2019). Its composition and diversity depend on the rhythms and timing of fruiting of forest stands. This stratum is subject to high mortality due to predation, parasitism, falling debris and changing environmental conditions (Baraloto, 2003; Kitajima & Fenner, 2000). The sapling stratum consists of woody individuals with a dbh between 1 and 10 cm (Gillet, 2013; Steven, 1994) and is composed by the biggest individuals emerging from the seedling stratum, selected by local ecological conditions, some of which may participate in replacing canopy trees.

It is expected that after human disturbance within a forest stand, the density, diversity and composition of the juvenile bank are significantly affected, due to species-specific ecological requirements. The microclimates resulting from each land use type can modify the expression of natural regeneration drivers and thus the trajectory taken by forest succession dynamics (Thompson et al., 2002; Poorter et al., 2016; Schwartz et al., 2017). The influence of land use type on the juvenile bank has been little studied, particularly in Africa. As in most parts of Central Africa, Cameroon's forests are subject to several types of land use, which can directly affect the ecological conditions of the forest understorey. There are three main types of land use: logging concessions, protected areas and community forests, which cover 29, 19 and 10% of the total forest area respectively. Each type is characterised by different intensities and frequencies of disturbance in space and time (Brown, 2004; Zhu et al., 2014; Poorter et al., 2016). To ensure appropriate management and ecosystem functionality, it is important to predict the response of plant communities to those different land use types.

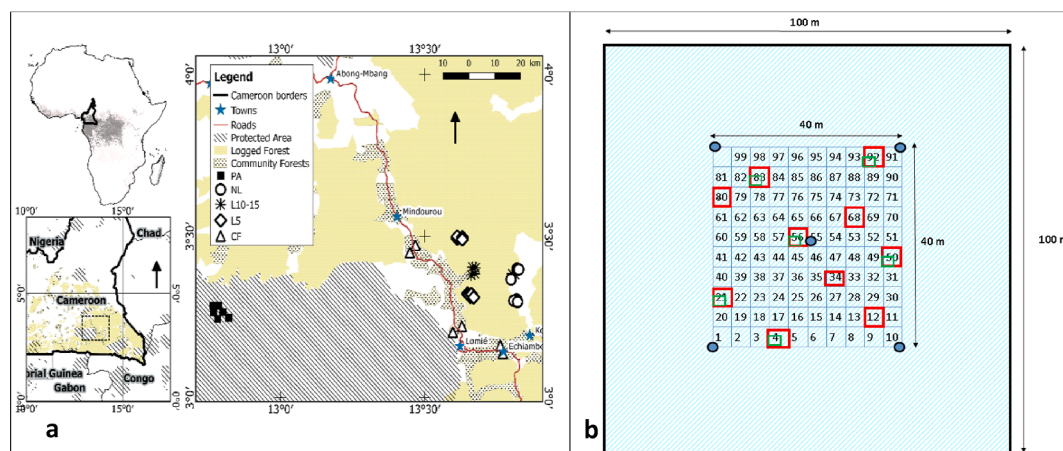
The objective of this study is to examine the diversity and composition of the forest understorey of south-eastern Cameroon along a gradient of presumed increasing human disturbance, defined as three land use types: (i) protected areas, (ii) selectively logged forests for timber, and (iii) community forests. More specifically, by following this gradient, this study: (i) describes the understorey vegetation in terms of functional groups and species composition, (ii) assesses its spatial variation in terms of density and diversity, and (iii) estimates its similarity with adjacent forest.

## 2. Materials and methods

### 2.1. Study area

This study was conducted in South-east Cameroon (Fig. 1) where the predominant vegetation is lowland semi-deciduous forest (average elevation 625 m) dominated by Malvaceae and Cannabaceae (ex Ulmaceae) (Letouzey, 1985). Due to the relatively flat topography, patches of periodically flooded forest and evergreen forest are also present (Letouzey, 1985). Rainfall varies annually from 1,500 to 2,000 mm and is mainly spread over two rainy seasons (>100 mm per month) from April to May and from September to December. The average temperature is 24 °C, and the relative humidity is about 75% throughout the year (Fick & Hijmans, 2017). The soils are mostly ferrallitic and are derived from the disintegration of the metamorphic parent rock (Segalen, 1967).

The understorey vegetation of this region was sampled along the human disturbance gradient highlighted by Lhoest et al. (2020), comprising three types of land use: (i) a protected area, (ii) a logging concession, and (iii) three community forests. The protected area is the Dja Biosphere Reserve (526,000 ha), characterised by abundant fauna, particularly active in seed dispersal. This forest area has never been exploited for timber, and its distance from villages makes it difficult to collect other forest products and thus limits its anthropisation. The logging concession is a production forest certified by the *Forest Stewardship Council* (FSC) for its responsible management and has been granted to the PALLISCO company since 2004 (341,708 ha). It is subject to selective timber harvesting: on average 0.65 stem or 9.6 m<sup>3</sup> of timber are harvested per hectare over a cutting cycle of 30 years following legal standards and management plan requirements. Other activities such as hunting and the collection of other forest products are controlled, and shifting cultivation is prohibited. Our sampling in this production forest has been subdivided into three groups: (i) never logged or logged more than 30 years before inventory (NL), (ii) logged 10–15 years before inventory (L10-15) and (iii) logged <5 years before inventory (L5; Fig. 1a). The three community forests belong to the villages Eschiambor (5,069 ha), Medjoh (4,964 ha) and Mintoum (3,433 ha). They are managed by local communities under the supervision of Cameroon's forest authorities and were logged 7–10 years before inventory. In these forests, the intensity of timber and non-timber forest product collection is higher due to the relatively higher population density and proximity to roads and villages (Lhoest et al., 2020). Slash-and-burn agriculture is



**Fig. 1.** (a) Location of the 33 permanent plots of one hectare each, representing the sampling units, in the different land use types of the South East Cameroon region. PA: Protected area, NL: Never logged forest or logged more than 30 years ago, L10-15: Forest logged 10–15 years ago, L5: Forest logged <5 years ago, CF: Community forest. (b) Configuration of a 1 ha permanent plot where: (i) all trees with a dbh ≥ 10 cm were inventoried; in a central area of 40 m × 40 m, (ii) trees, shrubs and lianas with a dbh between 1 and 10 cm were inventoried in 10 subplots of 4 m × 4 m (red squares); (iii) trees, shrubs, herbs and lianas with a dbh < 1 cm were inventoried in six 1 m × 1 m subplots (green squares); (iv) hemispheric photographs were taken (blue dots). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

widespread and human population density in the region is about 7 inhabitants/km<sup>2</sup>.

## 2.2. Vegetation inventory

Thirty-three plots of one hectare (100 m × 100 m) were set up in the three land use types. Satellite imagery and field observations were used to select sites that best reflected the different physiological variations observed in each land use type. These plots were at least 700 m apart (Fig. 1a). Six one-ha plots were set up in the protected area, 21 in the FSC-certified production forest (six for NL, six for L10-15, and nine for L5), and six in the community forests (Fig. 1a).

In each 1-ha plot, trees and shrubs with a dbh greater than or equal to 10 cm were identified to the species level and their diameter measured at 1.3 m from the ground (Picard et al., 2008). To assess vegetation with a dbh of <10 cm, an area of 40 m × 40 m was marked out in the centre of each one-hectare plot. In this core area, trees, shrubs and lianas with a dbh between 1 and 10 cm were surveyed in 10 randomly selected subplots of 16 m<sup>2</sup> each (4 m × 4 m) (red squares in Fig. 1b). Trees, shrubs, lianas with a dbh of <1 cm and herbaceous plants were surveyed in six randomly selected subplots of 1 m<sup>2</sup> (1 m × 1 m) (green squares in Fig. 1b). At the centre of each one-hectare plot, and then at four other equidistant points, located 28 m apart, canopy openness and leaf area index were measured from hemispherical photographs (Gond et al., 2002; Appendix 1).

The inventories were carried out between April 2015 and December 2018. Botanical reference specimens were collected to confirm the identifications proposed in the field. The verification was done at the Laboratory of Systematic Botany and Ecology (LaBosystE) of University of Yaoundé I and at the Herbarium of Université Libre de Bruxelles (ULB). Taxonomic nomenclature was checked and standardised using the African Plant Database (<https://www.ville-ge.ch/musinfo/bd/cjb/>) and The World Flora Online (<http://www.worldfloraonline.org/taxon>). Based on data from the literature, supplemented by our collective field experience, we classified the species into three regeneration guilds as proposed by Hawthorne (1995), Doucet (2003) and Meunier et al. (2015): pioneer (P), non-pioneer light demanding (NPLD) and shade-bearers (SB), and then into seven dispersal modes as proposed by Howe et Smallwood (1982): (i) Acanthochory with spiny, hooked or hairy diaspores; (ii) Ballochory with seeds ejected by the plant; (iii) Barochory with diaspores characterised mainly by their large mass and the absence of other dispersal structures; (iv) Pogonochory with diaspores with feathery or silky appendages; (v) Pterochory with diaspores with winged appendages; (vi) Sarcochory with diaspores with a soft, fleshy envelope; and (vii) Sclerochory with diaspores without special characteristics and a mass of <1 g.

## 2.3. Data analysis

Vegetation data were organised into four strata corresponding to: (i) woody and herbaceous individuals with dbh < 1 cm, (ii) woody individuals with dbh between 1 and 9.9 cm, (iii) woody individuals with dbh between 10 and 29.9 cm and (iv) woody individuals with dbh ≥ 30 cm. The tree life-forms individuals of these strata were named respectively: (i) seedlings, (ii) saplings, (iii) small trees, and (iv) large trees. Given the large variation in the number of individuals and the number of species among subplots, the density and diversity data of different strata were aggregated at the plot scale. The same was done for data of canopy openness, leaf area index, life-forms, regeneration guilds and dispersal syndromes.

To characterise each plot, canopy openness and leaf area index values, proportions of different life-forms (i.e., tree, shrub, liana and herbaceous), regeneration guilds and dispersal syndromes were determined within the different plots. Since the applicability conditions of ANOVA were not satisfied (normality verified by Shapiro's test and homogeneity of variances verified by Leuven's test), the non-parametric

Kruskal-Wallis test was used to verify whether land use types had a significant effect on these parameters. The median values for each land use type were compared using the Wilcoxon-Mann-Whitney test (95% confidence interval).

Within each understory vegetation stratum and for each land use type, the relative frequency (proportion of plots where the species is present), relative abundance (proportion of individuals belonging to a species compared to all individuals) as well as the ecological indicator value (*IndVal* and its significance at a threshold of 5% (Dufrene & Legendre, 1997)), were calculated for each species.

To compare the species composition between land use types for the understory vegetation strata, a NMDS (non-metric multidimensional scaling) was performed using the Bray-Curtis distance calculated on the basis of species abundance. Relationships between plot parameters (canopy openness, leaf area index, proportions of individuals of each life form, regeneration guild and dispersal syndrome) and ordination axes were quantified by multiple regression. The significance of the relationships was tested by a permutation test. The similarities in species composition between land use types were subsequently quantified by the Sorensen index (1-dissimilarity) (Faith et al., 1987).

The density of individuals was quantified as the sum of individuals counted per stratum in the subplots of a plot and then extrapolated to the hectare. The observed species richness of a plot was calculated as the sum of the different species recorded in the subplots. Predicted species richness was estimated using two non-parametric estimators, one based on abundance (S.chao1) and the other on incidence (S.ACE). Species diversity was estimated using the Shannon diversity index (sensitive to the distribution of the most abundant species) and the Simpson diversity index (sensitive to the distribution of the rarest species). The completeness of the sampling was assessed using the ratio S.obs/S.chao1 (observed species richness/estimated species richness). We also computed the observed species richness for each land use type, followed by extrapolation for the same number of individuals. To visualise the variation in species richness for a comparable number of samples, accumulation was performed using a reduced number of individuals randomly selected from each land use type.

A Moran's test was used to confirm the absence of spatial autocorrelation between plots for each index and an ANOVA was used to determine if individual density, observed and estimated species richness, and diversity were significantly different between land use types.

To assess the similarity between the understory vegetation (dbh < 1 cm and dbh 1–10 cm strata) and the adjacent forest stand (small trees and large trees), the dataset was restricted to individuals of tree species only. Given the difficulty in identifying some individuals in the seedling strata to species level, the composition of the juvenile bank (tree seedlings and saplings) was compared to that of the adjacent vegetation on the genus-scale reduced dataset. The indicator genera (*IndVal*) for the different strata were then determined.

Sorensen's similarity index (1-dissimilarity) (Faith et al., 1987) were computed to examine the similarity between strata. This was complemented by a NMDS (Bray-Curtis distance calculated from the abundance of genera) used to visualise the compositional similarity between these strata.

All analyses were performed using R (R CoreTeam, 2017). The *vegan* package was used for the study of species composition (Oksanen et al., 2019), *lme4* to calibrate and analyse the linear mixed models (Bates, 2016), *labdsv* to determine the indicator species (Roberts & Roberts, 2019), *MASS* for the NMDS representations (Ripley et al., 2020) and *iNEXT* for the interpolation and the extrapolation of species richness.

## 3. Results

### 3.1. Composition of the understory vegetation

#### 3.1.1. Functional groups and land use types

A total of 4,159 individuals (dbh < 10 cm) belonging to 418 species,

232 genera and 69 families were recorded in the understory of the 33 plots. Land use types significantly influenced Canopy openness ( $\chi^2 = 10.51$ , ddf = 4,  $p = 0.036$ ) and leaf area index ( $\chi^2 = 10.35$ , ddf = 4,  $p = 0.006$ ; Figure S2). Canopy openness was significantly higher in forests logged 10–15 years before inventory than in community forests, and leaf area index was significantly lower in forests logged 10–15 years before inventory than in protected areas.

Across all land use types, understory vegetation (dbh < 10 cm) mostly comprises tree species (65% trees, 20% shrubs, 5% lianas and 9% herbs), species which are shade-bearing during their early stages of development (77% SB, 11% NPLD and 12% P), and species whose diaspores are mainly disseminated by animals (74% sarchocores, 8% sclerochores, 7% ptelochores, 6% ballochores, others 2%; Table S1).

The life-forms and dispersal modes varied across land use types (respectively  $\chi^2 = 9.72$ , ddf = 4,  $p = 0.045$  for life-forms in dbh < 1 cm and  $\chi^2 = 12.78$ , ddf = 4,  $p = 0.012$  for dispersal syndromes in dbh between 1 and 10 cm; Fig. 2). The maximum proportions of trees were recorded in community forests (CFs), while the minimum was recorded in forests logged 10–15 years before inventory (L10-15; Fig. 2a). In the stratum with life forms between 1 and 10 cm dbh, the maximum proportions of barochores were recorded in CFs and the minimum in protected areas (PAs; Fig. 2b). None of the other differences in life form, regeneration guild or dispersal mode were significant.

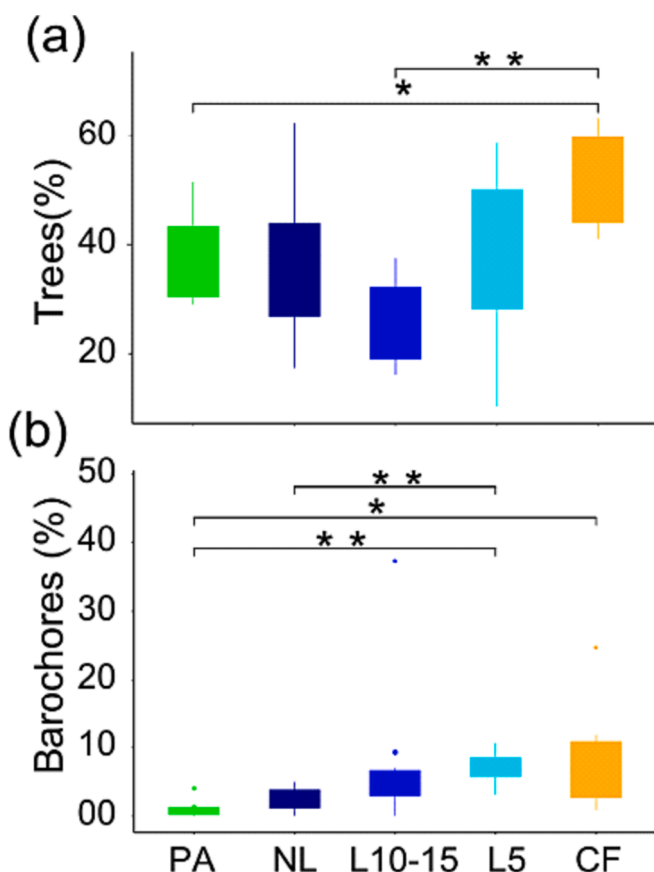


Fig. 2. Proportion of individuals of tree species in the stratum of individuals with dbh < 1 cm (a) and proportion of individuals of barochore species in the stratum of individuals with dbh between 1 and 10 cm (b) according to land use types. PA: Protected area; NL: forest logged more than 30 years before inventory; L10-15: forest logged 10–15 years before inventory; L5: forest logged <5 years before inventory and CF: forest logged 7–10 years before inventory. The asterisks (\*) and \*\*) correspond to crossed bars indicate pairs of land use types that are significantly different according to the Wilcoxon-Mann-Whitney test.

### 3.1.2. Species composition

The relative densities and frequencies of species vary considerably across strata and land use types (Table S1). The ten most frequent species (represented here by their relative frequency and relative density) for the dbh < 1 cm and dbh 1–10 cm strata are listed in Table 1. Overall, 27% of the inventoried species are present in both strata. There are 14 species exclusive to the dbh < 1 cm stratum, and 55 species exclusive to the dbh 1–10 cm stratum (Table S1).

The dbh < 1 cm stratum has as indicator species shade-bearing herbs (*Commelina* spp., *Geophila obvallata*, *Palisota ambigua*, *Palisota* sp.2), lianas (*Manniophyton fulvum*, *Cnestis* sp., *Landolphia* sp.) and some herbaceous species requiring large quantities of light for their development (*Haumania* sp., *Marantochloa* sp.). The dbh 1–10 cm stratum is characterised by shade-bearing tree and shrubby species (*Drypetes* sp., *Tabernaemontana crassa*, *Greenwayodendron suaveolens*, *Rinorea cuspa*, *Microdesmis* sp., *Carapa procera*; Table 1). Depending on land use types, the number of indicator species varies from 1 to 5 in the dbh < 1 cm stratum (in NL and L5 respectively) and from 0 to 9 in the dbh 1–10 cm stratum (in L10-15 and PAs respectively; Table 1).

Affinities are observed between plot parameters and the land use types (Fig. 3). In the dbh < 1 cm stratum, L5 is mainly composed of trees, shrubs, pioneer species, pogonochores and pterochores. In CF, species composition is mainly related to high leaf area, while in L10-15 it is related to the presence of shrubby and shade tolerant species. For the dbh 1–10 cm stratum, PA is mainly composed of shrubby, sarchocore and shade tolerant species. The CF is characterised with an abundance of barochorous species and a high leaf area. In contrast, L5 is related to an abundance of pterochorous species.

Except between forests logged 10–15 years before inventory and CFs in the dbh < 1 cm stratum (Sorensen = 0.29), there are no substantial similarities of species composition between the different plot groups. The Sorensen similarity index (1-dissimilarity) ranges from 0.29 to 0.52 within the dbh < 1 cm stratum and from 0.48 to 0.56 for the dbh 1–10 cm stratum (Table S2). Furthermore, the NMDS does not show a clear segregation of specific composition between land use types (Fig. 3). However, for all pairs of dimensions considered, plots belonging to the same land use types remain fairly clustered.

### 3.2. Richness and diversity of understory

A total of 1,126 individuals with dbh < 1 cm and 3,033 individuals with dbh between 1 and 10 cm were recorded. This corresponds to mean densities of  $5,687 \pm 1,422$  and  $5,744 \pm 1,554$  individuals per hectare respectively. The density of individuals with dbh < 1 cm, their observed species richness and diversity (Shannon and Simpson indices) were significantly different between land use types (Table 2). They were usually significantly higher in L5 and lower in NL. Within the forest concession there is a significant gradient between unlogged and recently logged forest (Table 2). Considering the estimated species richness there is no significant differences but it should be emphasised that the sampling at land use types level is not exhaustive; the  $S_{obs}/S_{chao1}$  ratio is between 39% and 48% for the dbh < 1 cm stratum and between 45% and 53% for the dbh 1–10 cm stratum (Table 2).

In addition, the rarefaction curves do not show asymptotes (Figure S1). However, they show the same pattern both when all sampled individuals are rarefied (Fig. S1a, c and e) or when the same reduced number of randomly selected individuals are rarefied (Fig. S1b, d and f).

### 3.3. Comparison of understory vegetation and adjacent vegetation

Considering only the 218 tree genera identified in the understory and adjacent vegetation (Table 3, Table S3). sapling indicator genera were *Massularia* (relative frequency = 0.39), *Microdesmis* (0.73), *Rinorea* (0.76), *Strychnos* (0.23). The small tree stratum had 122 indicator genera including *Anonidium* (0.96), *Corynanthe* (1.00), *Greenwayodendron*

**Table 1**

Indicator species (regeneration guild, life forms and dispersal syndromes) and 10 most frequent species (relative frequency; relative density) of each land use type and for all land use types (LUT) taken together (ALL) for the stratum of individuals with dbh < 1 cm and dbh between 1 and 10 cm. SB: shade-bearing, P: pioneer, NPLD: non-pioneer light demanding. Relative frequency: fraction of plots belonging to a group where the species is present. Relative Abundance: fraction indicating to what extent a species is only found in the considered group. Abbreviations; PA: protected area, NL: forest logged more than 30 years before inventory, L10\_15: forest logged 10–15 years before inventory, L5: forest logged <5 years before inventory and CF: community forest logged 7–10 years before inventory.

Stratum dbh < 1 cm			Stratum dbh between 1 and 10 cm		
LUT	Indicator species	Dominant species	Indicator species	Dominant species	
PA	<i>Strombosia</i> sp. (SB; Tree; Sarcochore), <i>Geophila macropoda</i> (SB; Herb; Sarcochore)	<i>Bertiera</i> sp. (0.83; 0.40), <i>Commelina</i> sp2 (0.83; 0.40), <i>Haumania</i> sp. (0.83; 0.26), <i>Strombosia</i> sp. (0.67; 0.80), <i>Microdesmis</i> sp. (0.67; 0.28), <i>Landolphia</i> sp. (0.67; 0.29), <i>Manniophyton</i> sp. (0.67; 0.21), <i>Marantochloa</i> sp. (0.67; 0.21), <i>Microdesmis</i> sp. (0.67; 0.28), <i>Palisota ambigua</i> (0.67; 0.22)	<i>Cola</i> sp. (SB; Tree; Sarcochore), <i>Coffea</i> sp3 (SB; Shrub; Sarcochore), <i>Centroplicus glaucinus</i> (SB; Tree; Sarcochore), <i>Desplatsia dewevrei</i> (SB; Tree; Sarcochore), <i>Dialium pachyphyllum</i> (SB; Tree; Sarcochore), <i>Grewia coriacea</i> (SB; Tree; Sarcochore), <i>Psychotria densinervia</i> (NPLD; Shrub; Sarcochore), <i>Dialium</i> sp. (SB; Tree; Sarcochore), <i>Chytranthus</i> sp. (SB; Tree; Sarcochore)	<i>Coffea</i> sp3 (1; 0.56), <i>Greenwayodendron suaveolens</i> (1; 0.23), <i>Drypetes</i> sp. (1; 0.15), <i>Centroplicus glaucinus</i> (0.83; 0.61), <i>Irvingia grandifolia</i> (0.83; 0.41), <i>Strombosia tetrandra</i> (0.83; 0.32), <i>Rinorea cuspa</i> (0.83; 0.17), <i>Microdesmis</i> sp. (0.83; 0.11), <i>Desplatsia dewevrei</i> (0.67; 0.66), <i>Dialium pachyphyllum</i> (0.67; 0.63)	
NL	<i>Myrianthus arboreus</i> (NPLD; Tree; Sarcochore)	<i>Marantochloa</i> sp. (0.83; 0.32), <i>Myrianthus arboreus</i> (0.83; 0.55), <i>Greenwayodendron suaveolens</i> (0.83; 0.38), <i>Tabernaemontana crassa</i> (0.50; 0.46), <i>Whitfieldia elongata</i> (0.50; 0.26), <i>Campylospermum</i> sp1 (0.50; 0.43), <i>Haumania danckelmaniana</i> (0.50; 0.38), <i>Trichilia</i> sp. (0.50; 0.45), <i>Commelina</i> sp	<i>Trichilia</i> sp. (SB; Tree; Sarcochore), <i>Dicranolepis pulcherrima</i> (SB; Shrub; Sarcochore)	<i>Drypetes</i> sp. (1; 0.15), <i>Greenwayodendron suaveolens</i> (0.83; 0.24), <i>Tabernaemontana crassa</i> (0.83; 0.16), <i>Trichilia</i> sp. (0.83; 0.63), <i>Irvingia grandifolia</i> (0.67; 0.13), <i>Strombosia tetrandra</i> (0.67; 0.24), <i>Rinorea cuspa</i> (0.67; 0.09), <i>Microdesmis</i> sp. (0.67; 0.23), <i>Strombosia pustulata</i> (0.67; 0.16), <i>Carapa procera</i> (0.67; 0.18)	
L10-15	<i>Cnestis</i> sp. (SB; Liana; Sarcochore)	<i>Hylodendron gabunense</i> (0.83; 0.17), <i>Cnestis</i> sp. (0.83; 0.50), <i>Marantochloa</i> sp. (0.67; 0.15), <i>Commelina</i> sp2 (0.67; 0.47), <i>Palisota ambigua</i> (0.67; 0.16), <i>Manniophyton</i> sp. (0.67; 0.24), <i>Whitfieldia elongata</i> (0.50; 0.45), <i>Landolphia</i> sp. (0.50; 0.33), <i>Trichilia prieuriana</i> (0.50; 0.75), <i>Geophila obvallata</i> (0.5; 0.38)		<i>Drypetes</i> sp. (1; 0.26), <i>Greenwayodendron suaveolens</i> (1; 0.21), <i>Tabernaemontana crassa</i> (1; 0.21), <i>Rinorea cuspa</i> (1; 0.30), <i>Trichilia welwitschii</i> (0.83; 0.22), <i>Strombosia tetrandra</i> (0.67; 0.21), <i>Strombosia pustulata</i> (0.67; 0.24), <i>Celtis mildbraedii</i> (0.67; 0.22), <i>Vepris louisii</i> (0.67; 0.41), <i>Hylodendron gabunense</i> (0.67; 0.24)	
L5	<i>Microdesmis</i> sp. (SB; Tree; Sarcochore), <i>Cercestis mirabilis</i> (SB; Herb; Sarcochore), <i>Coffea</i> sp1 (SB; Shrub; Sarcochore), <i>Cylicodiscus gabunensis</i> (P Tree; Pterochore), <i>Halopegia azurea</i> (P; Herb; Ballochore), <i>Hymenocoleus nervopilosus</i> (SB; Herb; Sclerochore)	<i>Microdesmis</i> sp. (0.89; 0.49), <i>Marantochloa</i> sp. (0.78; 0.24), <i>Manniophyton</i> sp. (0.78; 0.22), <i>Haumania</i> sp. (0.78; 0.21), <i>Greenwayodendron suaveolens</i> (0.78; 0.36), <i>Drypetes</i> sp. (0.78; 0.43), <i>Palisota ambigua</i> (0.67; 0.19), <i>Pterodo</i> sp. (0.67; 0.71), <i>Palisota</i> sp2 (0.56; 0.28), <i>Strombosia pustulata</i> (0.56; 0.31)	<i>Microdesmis</i> sp. (SB; Tree; Sarcochore), <i>Irvingia gabonensis</i> (SB; Tree; Sarcochore), <i>Octolobus</i> sp. (SB; Shrub), <i>Coffea</i> sp1 (SB; Shrub; Sarcochore), <i>Afzelia</i> sp (NPLD; Tree; Sarcochore)	<i>Microdesmis</i> sp. (1; 0.49), <i>Drypetes</i> sp. (0.89; 0.24), <i>Greenwayodendron suaveolens</i> (0.89; 0.21), <i>Tabernaemontana crassa</i> (0.89; 0.22), <i>Pausinystalia macroceras</i> (0.89; 0.41), <i>Rinorea cuspa</i> (0.78; 0.16), <i>Afrostryax lepidophyllus</i> (0.78; 0.28), <i>Manniophyton fulvum</i> (0.78; 0.17), <i>Petersianthus macrocarpus</i> (0.78; 0.33), <i>Irvingia gabonensis</i> (0.67; 0.60)	
FC	<i>Afrostryax lepidophyllus</i> (SB; Tree; Sarcochore), <i>Streblus usambarensis</i> (SB; Tree; Sarcochore), <i>Pseuderanthemum</i> sp.	<i>Palisota ambigua</i> (0.83; 0.28), <i>Hylodendron gabunense</i> (0.83; 0.39), <i>Manniophyton</i> sp. (0.67; 0.24), <i>Haumania</i> sp. (0.67; 0.20), <i>Strombosia pustulata</i> (0.50; 0.31), <i>Petersianthus macrocarpus</i> (0.50; 0.47), <i>Streblus usambarensis</i> (0.50; 0.82), <i>Monstera</i> sp. (0.50; 0.64), <i>Afrostryax lepidophyllus</i> (0.50; 0.82), <i>Haumania danckelmaniana</i> (0.50; 0.50), <i>Pseuderanthemum</i> sp	<i>Petersianthus macrocarpus</i> (NPLD; Tree; Pterochore), <i>Streblus usambarensis</i> (SB; Tree; Sarcochore), <i>Voacanga africana</i> (P; Shrub; Sarcochore), <i>Trichilia dregeana</i> (SB; Tree; Sarcochore), <i>Psychotria</i> sp. (NPLD; Shrub; Sarcochore), <i>Turraeanthus africanus</i> (SB; Tree; Sarcochore)	<i>Microdesmis</i> sp. (1; 0.165), <i>Tabernaemontana crassa</i> (1; 0.23), <i>Drypetes</i> sp. (0.83; 0.20), <i>Greenwayodendron suaveolens</i> (0.83; 0.12), <i>Petersianthus macrocarpus</i> (0.83; 0.45), <i>Anonidium mannii</i> (0.67; 0.34), <i>Santiria trimera</i> (0.67; 0.53), <i>Massularia acuminata</i> (0.67; 0.31), <i>Streblus usambarensis</i> (0.67; 0.92), <i>Voacanga africana</i> (0.67; 0.80)	
Stratum dbh < 1 cm			Stratum dbh between 1 and 10 cm		
LUT	Indicator species	Dominant species	Indicator species	Dominant species	
ALL	<i>Haumania</i> sp. (P; Herb), <i>Marantochloa</i> sp. (P; Herb; Sarcochore), <i>Palisota ambigua</i> (SB; Herb; Sarcochore), <i>Cnestis</i> sp. (SB; Liana; Sarcochore), <i>Palisota</i> sp2 (SB; Herb; Sarcochore), <i>Commelina</i> sp2 (NPLD; Herb; Sclerochore), <i>Landolphia</i> sp. (SB; Liana; Sarcochore), <i>Calamus</i> sp1 (NPLD; Herb; Sarcochore), <i>Geophila obvallata</i> (SB; Herb; Sarcochore), <i>Haumania danckelmaniana</i> (P; Herb; Ballochore)	<i>Haumania</i> sp. (0.67; 1), <i>Marantochloa</i> sp. (0.64; 1), <i>Palisota ambigua</i> (0.64; 1), <i>Hylodendron gabunense</i> (0.52; 0.67), <i>Cnestis</i> sp. (0.39; 1), <i>Palisota</i> sp2 (0.39; 1), <i>Landolphia</i> sp. (0.36; 0.89), <i>Bertiera</i> sp. (0.36; 0.55), <i>Commelina</i> sp2 (0.33; 1), <i>Psychotria</i> sp. (0.30; 0.64)	<i>Drypetes</i> sp. (SB; Shrub; Sarcochore), <i>Tabernaemontana crassa</i> (SB; Tree; Sarcochore), <i>Greenwayodendron suaveolens</i> (SB; Tree; Sarcochore), <i>Rinorea dentata</i> (SB; Tree; Sclerochore), <i>Microdesmis</i> sp. (SB; Tree; Sarcochore), <i>Carapa procera</i> (SB; Tree; Sarcochore), <i>Anonidium mannii</i> (SB; Tree; Sarcochore), <i>Strombosia tetrandra</i> (SB; Tree; Sarcochore), <i>Strombosia pustulata</i> (SB; Tree; Sarcochore), <i>Irvingia grandifolia</i> (SB; Tree; Sarcochore), <i>Maesophagus</i> (SB; Tree; Sarcochore), <i>Maesophagus</i> sp; Sarcochore), <i>Maesobotrya klaineana</i> (SB; Tree; Sarcochore), <i>Anthonotha macrophylla</i>	<i>Drypetes</i> sp. (0.94; 0.90), <i>Greenwayodendron suaveolens</i> (0.91; 0.81), <i>Tabernaemontana crassa</i> (0.88; 0.93), <i>Rinorea dentata</i> (0.76; 0.90), <i>Microdesmis</i> sp. (0.73; 0.88), <i>Strombosia pustulata</i> (0.64; 0.73), <i>Strombosia tetrandra</i> (0.64; 0.82), <i>Carapa procera</i> (0.61; 1), <i>Anonidium mannii</i> (0.56; 1), <i>Anthonotha macrophylla</i> (0.42; 1)	

(continued on next page)

Table 1 (continued)

Stratum dbh < 1 cm			Stratum dbh between 1 and 10 cm	
LUT	Indicator species	Dominant species	Indicator species	Dominant species
			(SB; Tree; Ballochore), <i>Trichilia welwitschii</i> (SB; Tree; Sarcochore), <i>Coffea</i> sp2 (SB; Tree; Sarcochore), <i>Campylosperrum mannii</i> (SB; Tree; Sarcochore)	

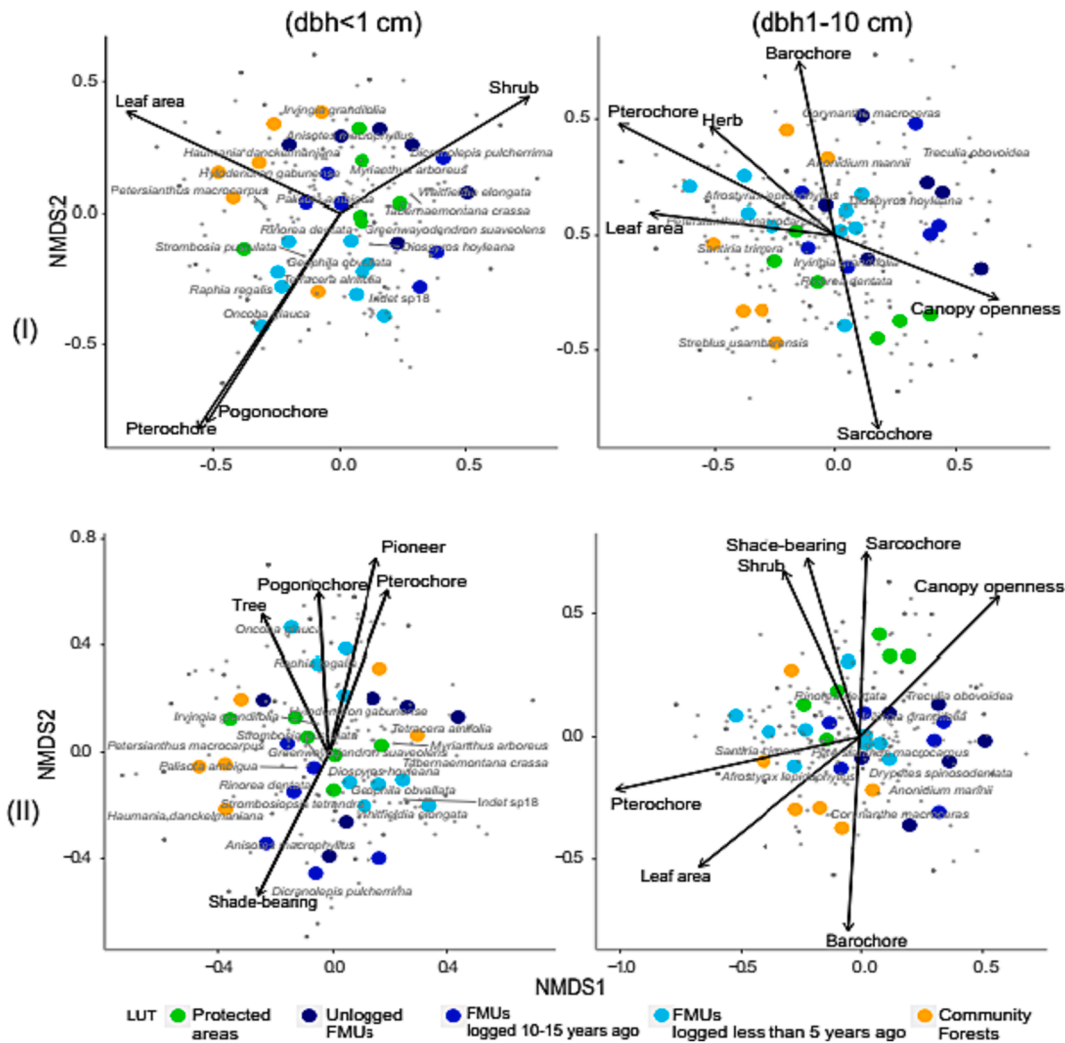


Fig. 3. Main dimensions (represented by I and II) of the Nonmetric Multidimensional Scaling (NMDS) for individuals with dbh < 1 cm and those with dbh between 1 and 10 cm. Each coloured point corresponds to a parcel and the colours refer to a type of land use. The grey dots correspond to the species. Only the names of taxa identified to the species level among the 20 most abundant are displayed. Environmental parameters significantly correlated with the main dimensions of each ordination (I and II) are projected as additional variables (permutation test, 0.05).

(1.00), *Irvingia* (1.00), *Santiria* (1.00), *Strombosia* (1.00), *Sorindeia* (0.96), *Strombosiosis* (0.96), *Tabernaemontana* (0.96), and *Trichilia* (0.96). For large trees, the indicator genera were *Alstonia* (0.67), *Petersianthus* (0.94), *Distemonanthus* (0.15), and *Terminalia* (0.39).

The seedling stratum is less similar to the standing vegetation (Sorensen: 0.45 to 0.48) than the sapling stratum (Sorensen: 0.74; Table 4). These observations are confirmed by a NMDS. There is a clear segregation between the juvenile strata and the adjacent vegetation. Logically, the seedling bank seems to be closer to the sapling bank than to the small and large tree strata (Fig. 4).

#### 4. Discussion

Natural regeneration of tropical rainforests is a complex process involving various biotic and abiotic factors. By describing the diversity and composition of the understory vegetation, this study assessed the forest dynamics of the main land use types in the South-east Cameroon region. The effect of an anthropisation gradient on seedling and sapling communities was investigated. Indicators that were supposed to reflect the anthropisation gradient were found to be not representative: canopy openness was highest in forests logged 10–15 years before inventory and leaf area index was highest in community forests logged 7–10 years before inventory. We found that the proportion of young trees in the understory was highest in community forests (67% trees, 14% shrubs,

**Table 2**

Mean values ( $\pm$ standard deviation) of the density of individuals (N.dens), observed (S.obs) and estimated (S.Chao1, S.ACE) and diversity (Shannon and Simpson) of the stratum of individuals with dbh < 1 cm (dbh < 1) and those with dbh between 1 and 10 cm (dbh\_1-10), according to land use types. The *p*-values show the significance of the ANOVA testing the effect of the land use types for each index and within each stratum. The S.obs/S.Chao1 ratio illustrates the sampling effort. Abbreviations; PA: protected area, NL: forest logged more than 30 years before inventory, L10\_15: forest logged 10–15 years before inventory, L5: forest logged <5 years before inventory and CF: community forest logged 7–10 years before inventory.

	dbh < 1					<i>p</i>	dbh_1-10					<i>p</i>
	PA	NL	L10-15	L5	CF		PA	NL	L10-15	L5	CF	
<b>N.dens</b>	5472 $\pm$ 499 (b)	4639 $\pm$ 933 (b)	4722 $\pm$ 1298 (b)	<b>7074 <math>\pm</math> 1414 (a)</b>	5833 $\pm$ 983 (b)	<b>0.0013</b>	5698 $\pm$ 1413	4521 $\pm$ 1576	5125 $\pm$ 1233	6680 $\pm$ 1516	5645 $\pm$ 1456	0.386
<b>S.obs</b>	24 $\pm$ 3 (ab)	19 $\pm$ 5 (c)	20 $\pm$ 4 (bc)	<b>28 <math>\pm</math> 6 (a)</b>	22 $\pm$ 3 (bc)	<b>0.0011</b>	43 $\pm$ 6 (ab)	32 $\pm$ 9 (c)	36 $\pm$ 8 (bc)	<b>47 <math>\pm</math> 7 (a)</b>	37 $\pm$ 9 (bc)	<b>0.0125</b>
<b>S.Chao1</b>	56 $\pm$ 34	42 $\pm$ 23	50 $\pm$ 31	68 $\pm$ 39	45 $\pm$ 13	0.510	96 $\pm$ 56	62 $\pm$ 28	72 $\pm$ 25	92 $\pm$ 32	70 $\pm$ 20	0.694
<b>S.ACE</b>	62 $\pm$ 32	52 $\pm$ 34	56 $\pm$ 21	70 $\pm$ 32	52 $\pm$ 17	0.568	93 $\pm$ 34	69 $\pm$ 27	84 $\pm$ 35	109 $\pm$ 22	83 $\pm$ 27	0.185
<b>S.obs/S.Chao1</b>	0.43	0.44	0.39	0.42	0.48		0.45	0.52	0.50	0.51	0.53	
<b>Shannon</b>	3.06 $\pm$ 0.14 (ab)	2.77 $\pm$ 0.27 (c)	2.83 $\pm$ 0.16 (c)	<b>3.19 <math>\pm</math> 0.22 (a)</b>	2.92 $\pm$ 0.12 (bc)	<b>&lt;0.0001</b>	<b>3.46 <math>\pm</math> 0.08 (a)</b>	2.99 $\pm$ 0.38 (b)	3.12 $\pm$ 0.23 (ab)	<b>3.42 <math>\pm</math> 0.18 (a)</b>	3.12 $\pm$ 0.39 (ab)	<b>0.0041</b>
<b>Simpson</b>	19.21 $\pm$ 2.91 (ab)	14.33 $\pm$ 4.50 (c)	14.56 $\pm$ 1.54 (c)	<b>21.37 <math>\pm</math> 4.11 (a)</b>	15.71 $\pm$ 1.88 (bc)	<b>&lt;0.0021</b>	<b>22.42 <math>\pm</math> 2.78 (a)</b>	14.17 $\pm$ 6.82 (b)	14.67 $\pm$ 4.07 (ab)	<b>20.55 <math>\pm</math> 4.89 (a)</b>	15.71 $\pm$ 5.58 (ab)	<b>0.035</b>

**Table 3**

Table showing the average characteristics of the plots within the strata inventoried. The species richness (S.obs), genera and families are those observed on the surveyed area.

Strata	DBH classes	Basal area (m <sup>2</sup> /ha)	Density (individuals/ha)	Density of wood/ha	Quadratic mean diameter (cm)	S.obs/ha	Genera/ha	Families/ha
<b>Seedlings</b>	[0;1[	/	3884 $\pm$ 1359	0.63 $\pm$ 0.03	/	16 $\pm$ 5	15 $\pm$ 5	13 $\pm$ 3
<b>Saplings</b>	[1;10[	5.18 $\pm$ 1.30	5712 $\pm$ 1564	0.64 $\pm$ 0.02	0.43 $\pm$ 0.05	40 $\pm$ 9	35 $\pm$ 8	22 $\pm$ 5
<b>Small trees</b>	[10;30[	8.60 $\pm$ 1.59	383 $\pm$ 70	0.62 $\pm$ 0.04	16.93 $\pm$ 0.064	91 $\pm$ 14	76 $\pm$ 11	34 $\pm$ 4
<b>Large trees</b>	[30;+]	19.92 $\pm$ 4.00	87 $\pm$ 16	0.61 $\pm$ 0.06	54.30 $\pm$ 5.52	41 $\pm$ 7	38 $\pm$ 6	20 $\pm$ 3

**Table 4**

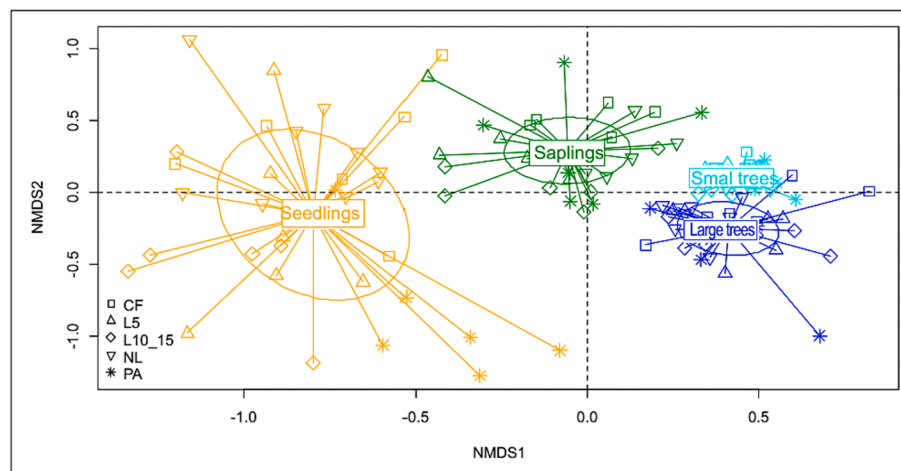
Similarity (Sorensen's index) of genera composition between different strata of juveniles (seedlings and saplings) and adjacent vegetation (small and large trees).

	Seedlings	Saplings	Small trees
<b>Saplings</b>	0.60		
<b>Small trees</b>	0.45	0.74	
<b>Large trees</b>	0.48	0.74	0.86

8% lianas and 11% herbs), which are the most disturbed forests. Specific compositions varied slightly among land use types without being clearly separated. The density and diversity of understorey species were highest in recently logged forests (Table 2). In the studied forest concession, both density and species diversity were negatively correlated with the time since last logging. Finally, the similarity between seedlings and other strata was lower (0.45–0.60) than the similarity between saplings and other strata (0.60–0.74).

4.1. Land use types and tree cover

Land use in our study area affected canopy openness and leaf area



**Fig. 4.** NMDS showing the genus composition of the seedling strata, the sapling strata, the small tree strata and the large tree strata at the plot level. PA: Protected area; NL: forest logged more than 30 years before inventory; L10\_15: forest logged 10–15 years before inventory; L5: forest logged <5 years before inventory and CF: forest logged 7–10 years before inventory.

index. These results contrast with those of Nicotra et al. (1998) in different forests in Costa Rica. Despite observing differences in canopy gap sizes between anthropized sites (see also Pinagé et al., 2019) with time steps of 5 years, they found no significant difference in the rate of canopy openness between these sites. Moreover, they reported maximum canopy openness in undisturbed forests. The fact that canopy openness is greater in forests that were selectively logged for timber 10–15 years before inventory could be explained by the death of fast-growing species (Fig. 2).

Indeed, generally after forest degradation, the mono-dominant light demanding species (*Musanga cecropioides*, *Macaranga* spp. and *Trema orientalis*) grow very rapidly, reaching more than four metres in two years (Kouadio & Doucet, 2009). They form a canopy under which shade-bearing species develop (Swaine & Whitmore, 1988; Baraloto, 2003; Peyrot, 2008). These short-lived pioneer light demanding species generally survive <20 years (Swaine & Hall, 1983) and give way to non-pioneer, shade-bearing species (Alexandre, 1989; Canham et al., 1990; Peyrot, 2008). This could also explain the greater light heterogeneity (observable by the large standard deviations in our sites) in selectively logged forests compared to forests which have never been logged (Figure S2). This observation can be explained by the high selectivity of logging creating a spatial succession of disturbed and undisturbed areas.

The higher leaf area index observed in the community forests (Figure S2) seems to reflect a rapid complexification of the vegetation structure after major environmental disturbances. In forests subjected to different types of logging, Asner et al. (2004) observed through spatial images that more than two thirds of the area of gaps in Brazilian rainforests is recolonized in the first three years after the disturbance. This recolonization is greater in community forests and recently logged forests, as these forests have a more closed canopy than others.

Under natural conditions, the vertical stratification of forests makes that <2% of incident solar radiation above the canopy reaches the understory (Chazdon & Pearcy, 1988; Sist & Brown, 2004). Changes affecting the canopy are therefore able to alter the composition and diversity of the understory vegetation (Alexandre, 1989; Valverde & Silvertown, 1997; Foster et al., 2003; Carson & Schnitzer, 2008; Yang et al., 2014). Tree death and fall, particularly as a result of site anthropisation, can affect light distribution in the understory (Asner et al., 2004). Gaps contribute to create favourable microclimates for development of fast-growing plants (Canham et al., 1990; White et al. Pickett, 1985).

#### 4.2. Main characteristics of the understory vegetation

In this study, we observed high proportions of shade-bearing species and animal-dispersed tree species in understory vegetation. These observations are common in tropical regions (Alexandre, 1989; Baraloto, 2003; Comita et al., 2007; Dent et al., 2013) and characterise forests with low-disturbance understory (Wright et al., 2003). Shade-bearing species are generally less subject to predation (Baraloto, 2003) and are characterised by large seed production (Foster 1982) germinating into seedlings that develop and persist for several years in the understory (Westoby et al., 1996).

In the dbh < 1 stratum, the significantly high proportions of tree individuals in community forests could be explained by a strong regeneration of light demanding species after major environmental disturbances (Bekker et al., 1998; Zebaze et al., 2021), in addition to the initially present shade species. However, this dynamic cannot be generalised as it is closely related to the periodicity and intensity of the disturbance, which is generally related to the population density of the area and related human activities (Lhoest et al., 2020).

The composition of the dbh 1–10 cm stratum did not vary between land use types, probably because this stratum is less sensitive to variations in environmental conditions and phenological phases. This stratum is formed by the recruitment and accumulation of individuals better adapted to the understory (Alexandre, 1989; Baraloto, 2003). These

latter elements make the dbh 1–10 stratum the most species-rich and diverse, but also the one with the most characteristic and indicator species (Kanagaraj et al., 2011). However, the abundance of indicator species observed within the different land use types could be over-estimated due to easier identification of individuals in this stratum.

Logging in our study area has increased, or at least not decreased, the floristic diversity of the plots. This observation has also been made by several authors (Battles et al., 2001; Carson & Schnitzer, 2008; Peyrot, 2008; Draper et al., 2021) and could be explained by new environmental conditions resulting from the disturbance of the milieu over relatively variable periods of time. These new conditions would favour the development of some groups of species, particularly according to their light requirements. In addition to the species present before the disturbance, the disturbance favours the development of newly dispersed pioneer species (Alexandre, 1989; Baraloto, 2003) and those present in the seed bank (Zebaze et al., 2021). This result shows the importance of the understory in maintaining biodiversity, but also highlights a regeneration deficit of light-demanding canopy species, including timber species (for example *Distemonanthus benthamianus* or *Terminalia superba*).

#### 4.3. Density and diversity of the understory

Although higher than in the surrounding vegetation (Table 3, Table S3), the densities of understory individuals observed in this study are five to twelve times lower than those observed by Comita et al. (2007) in Panama and by Harms et al. (2004) in a study conducted in Costa Rica, Panama, Peru and Brazil. In addition to the high density of individuals characteristic of South American rainforests (Turner, 2004; Bastin et al., 2018; de Miranda et al., 2022), these differences can be explained by a combination of factors affecting the distribution, recruitment, survival or removal of individuals in the understory strata. For example, by contrast to our results, Doucet (2003) observed in the continental rainforest of Gabon, seventeen times more woody individuals per hectare in the understory of a site that had been logged four years earlier.

The dbh < 1 cm stratum is very sensitive to variations in environmental conditions. Its individual density depends, among other, on (i) the specific composition of the site vegetation and the seasonality of seed production, (ii) the variation of light conditions, as well as (iii) the history of anthropisation (Augspurger, 1984; Steven, 1994; Peyrot, 2008). In the tropics, seed production and seedling survival are highly asynchronous and vary among species, sites and seasons (Steven, 1994; De Steven & Wright, 2002; Comita et al., 2007). The survival and growth of individuals in this strata contribute to the formation of those in the dbh 1–10 cm stratum.

The dbh 1–10 cm stratum is more stable and has a higher density of individuals than the preceding one. These observations are consistent with those of Kanagaraj et al. (2011) and Turner (2004), and would be due to the fact that this stratum is formed by the accumulation of individuals from the dbh < 1 cm stratum and the survival of the individuals best adapted to this environment (Kanagaraj et al., 2011).

Moreover, anthropisation does not lead to a reduction in richness or diversity, with both variables reaching maximum values in forests logged five years earlier. In fact, opening up the environment seems to allow the emergence of seedlings from the soil seed bank as well as the development of plants that remained in the understory. The low logging intensity results in little canopy opening in our study area. Dupuis et al. (in press) showed that, on average, logging gaps cover only 3.88% of the logged area. This low openness allows species from different regeneration guilds to coexist. Subsequently, light conditions in the understory decrease, making germination of pioneer species less likely.

#### 4.4. Juveniles and similarities with standing vegetation

In the understory vegetation, 65% of individuals are arborescent



species. These juveniles play a crucial role in gaps recovery (Uhl et al., 1988; Thompson et al., 2002; Dent et al., 2013). The 12% of species that are exclusively juvenile would confer on them a role of memory for the biological diversity of arborescent species; they would allow the regeneration of species that are now extinct in the surrounding vegetation, species that are long-distance dispersers and/or species that are poorly adapted to canopy conditions.

However, the low similarity observed between the seedling stratum and the small or large tree strata indicate a regeneration deficit for many species. In fact, the proportion of species exclusive to the standing vegetation (21% of species exclusive to the small tree stratum and 2% to the large tree stratum) would be due to adaptive specificities that allow (or not) the development of some species in contrasting environments. These specificities would include: (i) the regeneration guild of species; significant differences in light requirements are observed for exclusive species according to the strata. Indeed, 43% of the exclusive species in the seedling stratum are shade tolerant, whereas 74% in the sapling stratum, 51% in small trees and 28% in large trees are shade tolerant (Table S3). (ii) Number and type of diaspores; the diaspores produced by these species are mainly sarcochorous, not very dormant and germinate quickly in the understorey (Kitajima & Fenner, 2000; Chazdon & Guariguata, 2016) before being limited in their seedling density by natural selection (only 1% of individuals survive the environmental conditions and move to the next stratum; Carson & Schnitzer, 2008; Baraloto, 2003). The combination of these factors explains why some species that dominate the canopy once regenerated in fields abandoned by farmers decades ago when shifting cultivation was widespread in the region (Vleminckx et al., 2017; Sullivan et al., 2022). Agriculture is today prohibited in logging concessions and protected areas, as a result the composition of the understorey vegetation changed.

The clear distinction in genus composition observed between plant communities for seedlings, saplings and adjacent vegetation highlights the specificity of each stratum in the process of forest dynamics. Theoretical studies show that limited recruitment can maintain local diversity by allowing competitively disadvantaged species to persist in some strata where favoured species are absent (Chave, 2000; Carson & Schnitzer, 2008). This supports the idea of strong stratification in tropical environments and the fact that secondarised forest only returns to its original state after several decades (Alexandre, 1989; Baraloto, 2003; Peyrot, 2008).

Although the variation is very small (<10% on Sorensen's index), these results remain unchanged when compared at the species level (see also Figure S3; Table S4). However, these observations may be limited by the difficulty of accurately identifying all seedlings and some saplings. In addition, many species complete their life cycle in the understorey; their DBH rarely exceeds 10 cm. This is particularly the case for all indicative genera found in the sapling stratum (Table S3).

## 5. Conclusion

In this study, we showed that only 16% of species were present in all strata, reflecting the low similarity between juveniles and adjacent vegetation. The understoreys of the forests that had been logged five years earlier were the densest and most diverse. However light-demanding timber species were rare or absent. To maintain this species on the long-term, enrichment plantings are necessary. Further studies are needed to identify the tipping point of forest dynamics in a landscape with different land uses since our study site was characterized by a low logging intensity and a low human density.

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## CRedit authorship contribution statement

**Donatien Zebaze:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Visualization, Writing – original draft, Funding acquisition. **Anaïs Gorel:** Conceptualization, Formal analysis, Data curation, Visualization, Writing – review & editing. **Jean-François Gillet:** Investigation, Resources, Writing – review & editing, Visualization. **Fructueux Houngbégnon:** Formal analysis, Resources, Validation, Writing – review & editing, Visualization. **Nicolas Barbier:** Investigation, Resources, Writing – review & editing, Visualization. **Gauthier Ligot:** Conceptualization, Formal analysis, Validation, Writing – review & editing, Visualization. **Simon Lhoest:** Formal analysis, Writing – review & editing, Visualization. **Gyslène Kamdem:** Investigation, Resources, Visualization, Writing – review & editing. **Moses Libalah:** Investigation, Writing – review & editing, Visualization. **Vincent Droissart:** Supervision, Visualization, Writing – review & editing, Visualization. **Bonaventure Sonké:** Conceptualization, Supervision, Visualization, Writing – review & editing, Funding acquisition. **Jean-Louis Doucet:** Conceptualization, Methodology, Formal analysis, Supervision, Validation, Visualization, Writing – review & editing, Visualization, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121402>.

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